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The Development and Application of a Larval Pallid Sturgeon (Scaphirhynchus albus) Bioenergetics Model

Laura B. Heironimus
South Dakota State University

THE DEVELOPMENT AND APPLICATION OF A LARVAL PALLID STURGEON (*SCAPHIRHYNCHUS ALBUS*) BIOENERGETICS MODEL

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LAURA B. HEIRONIMUS

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This thesis is approved as a creditable and independent investigation by a candidate for the Master of Science in Wildlife and Fisheries Sciences degree and is acceptable for meeting the thesis requirements for this degree. Acceptance of this thesis does not imply that the conclusions reached by the candidate are necessarily the conclusions of the major department

Steven Chipps, Ph.D.
Thesis Advisor Date

Nels Troelstrup, Ph.D
Head, Department of Natural Resource Management Date

Dean, Graduate School Date

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ABSTRACT

THE DEVELOPMENT AND APPLICATION OF A LARVAL PALLID STURGEON (*SCAPHIRHYNCHUS ALBUS*) BIOENERGETICS MODEL

LAURA B. HEIRONIMUS

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Pallid Sturgeon *Scaphirhynchus albus* are native fish of the Missouri and lower Mississippi River basins and currently listed as an endangered species under the Federal Endangered Species Act. As a result of anthropogenic alterations within the Missouri River, including dredging, channelization, and construction of large reservoirs, Pallid Sturgeon reproduction is reduced or eliminated throughout the species range. Due to a lack of wild progeny, little is known of the larval Pallid Sturgeon and their habitat or environmental requirements. To increase knowledge on the larval Pallid Sturgeon's physiological requirements for growth and survival, the objective of this study was to develop a bioenergetics model to determine optimal temperature for growth of young-of-year Pallid Sturgeon and apply the model in a realistic simulation. To develop this model, I estimated metabolic demands and growth over a range of temperatures and sizes. Pallid Sturgeon (0.005 to 9.094 g) were subjected to a range of temperatures commonly found in the Missouri River (13 – 28°C). Exogenously feeding larval fish were fed chironomids at *ad libitum* rations three times daily over multiple days to determine maximum consumption and estimate growth. I used static respirometry to quantify the routine respiration rate of larval Pallid Sturgeon. Using this model, I estimated daily consumption (g/d) for a 1-g fish, ranging from 0.15 g/d at 13°C to 0.31 g/d at 24°C. I also estimated daily oxygen consumption (M, g O_2/d) of a 1-g larval fish

to range from 0.006 g O_2/d at 13°C to 0.016 g O_2/d at 28°C. The independent observations of daily consumption (g/d) fit the bioenergetic estimates of daily consumption ($F_{2,35}$= 477, r^2 = 0.96, P-Value < 0.001). I then used the bioenergetics model to simulate and compare growth potential between historical and contemporary water temperatures in two reaches of the Missouri River. For these simulations I looked at the difference in end weights in a Spawning Scenario, estimating larval growth across a growing season starting from hatch, and a Stocking Scenario, estimating larval growth across a growing season starting with larvae stocked on July 1st. Temperature data were collected from Booneville, Missouri, hereafter referred to as the lower Missouri River (LMR) and Bismarck, North Dakota, hereafter referred to as the Garrison Reach (GR). In the Spawning Scenario, with feeding rate set at 50 % maximum consumption, I found a 1.0 % increase and a 65.2 % decrease in end weights from the Pre-Dam to Post-Dam time periods in the LMR and GR, respectively. This simulation resulted in 4.1 % fewer days and 5.0 % fewer cumulative thermal units (CTU) in the LMR and 38.3 % fewer days and 53.6 % fewer CTU in the GR. In the Stocking Scenario, with a feeding rate set at 50% maximum consumption, I found a 7.5 % increase and 37.4 % decrease in end weights from the Pre-Dam to Post-Dam time periods in the LMR and GR, respectively. This simulation resulted in 1.1 % fewer CTU in the LMR and 24.1 % fewer CTU in the GR. Our findings suggest that the cold waters of the deep-release storage reservoirs could negatively impact the growth potential of larval Pallid Sturgeon within at least 110 km downstream proximity; however, at approximately 960 km below impoundment, the negative impacts from temperature are no longer detected. With six major dams along the main stem upper Missouri River, thermal depression may be a leading cause of

recruitment failure in Pallid Sturgeon and I recommend additional research into the geographic range of cold water impacts on larval Pallid Sturgeon growth and survival.

CHAPTER 1. INTRODUCTION

Current Status and Research Needs

Pallid Sturgeon *Scaphirhynchus albus* are endemic large-bodied fish of the Missouri and lower Mississippi River basins. First described in 1905, little is known of the Pallid Sturgeon's early abundance and distribution (Pflieger et al. 1975). In 1989, the U.S. Army Corps of Engineers consulted with the U.S. Fish and Wildlife Service under provisions of section 7 of the Endangered Species Act regarding operation of the Missouri River Main Stem Reservoir System (USFWS 2003). After careful consideration, the U.S. Fish and Wildlife Service found that sturgeon habitat has been greatly modified by anthropogenic activities such as impoundment, dredging, and channelization (Hesse and Mestl 1993; Galat et al. 1998). As a result, reproduction has been reduced or eliminated throughout the species range (Dryer and Sandvol 1993; Bergman et al. 2008). Additional evidence of hybridization with the closely related Shovelnose Sturgeon *S. platorynchus* put the Pallid Sturgeon at risk of genetic extinction through introgressive hybridization (55 Fed. Reg. 36641-36647; Dryer and Sandvol 1993; Rhymer and Simberrloff 1996; Schrey et al. 2011). This combination of evidence prompted the listing of Pallid Sturgeon under the Endangered Species Act in 1990 (55 Fed. Reg. 36641-36647).

To better assess and manage Pallid Sturgeon, the geographical range has been partitioned into four management units: Great Plains, Central Lowlands, Interior Highlands, and Coastal Plain (Bergman et al. 2008). The boundaries of these management units are primarily dependent on the current genetic and stock structure data (USFWS 2014). Additionally, these management units are representative of the

boundaries in large-river fish communities (Bergman et al. 2008) and represent speciation associated with physiographic provinces (Metcalf 1966, Wiley and Mayden 1985, Burr and Page 1986, Cross et al. 1986). Within the geographic range of Pallid Sturgeon, impoundments cover an estimated 28% of the habitat, while 21% of the remaining un-impounded habitat is affected by upstream impoundments, altered flow regimes, decreased turbidity, altered water temperatures, and bank stabilization (Bergman et al. 2008). Additionally, population connectivity between Management Units is sufficiently low so that each population must be monitored and managed separately (Taylor and Dizon 1999).

The successful reproduction of large river fish, such as the Pallid Sturgeon, has been impeded by changes in timing, magnitude, and frequency of flow (USFWS 2003). Long-term recovery and maintenance of this species will likely require significant habitat restoration, with an emphasis on spawning and nursery habitat (DeLonay et al. 2009). Due to the critical status of the Pallid Sturgeon, short-term recovery efforts have focused primarily on propagation of juvenile fish. The primary goals of the artificial propagation program are to (1) supplement the population within each management unit, establishing multiple year classes and reducing the threat of local extirpation, (2) establish or maintain populations within the species' historic range, (3) maintain the genetic structure of the population by mimicking wild population haplotype or genotype frequencies in hatchery progeny, and (4) prevent the introduction of disease to the wild population (USFWS 2008). Although much has been learned about propagation and rearing techniques, comparatively little is known about habitat suitability for larval and juvenile Pallid Sturgeon (Kallemeyn 1983; Bergman et al. 2008). On the other hand, in the past decade

literature on sub-adult and adult Pallid Sturgeon habitat suitability has increased dramatically (USFWS 2014).

To date, larval Pallid Sturgeon research has focused primarily on parameterizing habitat requirements and drift dynamics within the Missouri and Mississippi Rivers. This focus is largely due to the 2003 U.S. Fish and Wildlife Service Amended Biological Opinion in which the U.S. Army Corps of Engineers was mandated to restore 1,200 additional acres of shallow water habitat for the larval Pallid Sturgeon (USFWS 2003). As a result of these studies, researchers have begun to understand factors affecting drift dynamics, feeding preferences, and survival of young Pallid Sturgeon (USFWS 2014). For 5-14 days post-hatch (dph) larvae, mean drift velocity ranges from 0.7 m s^{-1} to 0.66 m s^{-1} (Braaten et al. 2011). The transition from drifting to settling is initiated at about 18 mm and completed by 20 mm (Braaten et al. 2008). Based on drift velocity and time to settling, models suggests that larval Pallid Sturgeon have a drift distance ranging from of 245 to 530 km (Kynard et al. 2007; Braaten et al. 2008; Braaten et al. 2011). Using fin ray microchemistry, Phelps et al. (2012) found age- 0 *Scaphirhynchus* spp. larvae in the middle Mississippi River to have emigrated as far as 589 km from the lower Missouri River. Once settled in the middle Mississippi River, age-0 Pallid Sturgeon have been found in areas of low velocity (i.e., ~0.1 m/s), moderate depths (i.e., 2–5 m) and in channel-border dike and island side-channel macrohabitats (Phelps et al. 2010). A few free embryo Pallid Sturgeon have been identified in the Mississippi and Yellowstone Rivers and there is evidence for limited recruitment in the lower Missouri and Mississippi Rivers (Hrabik et al. 2007; USFWS 2014). Although considerable information has been gathered since listing, the cause of recruitment failure is still unknown. Additional

information, such as foraging behavior, temperature tolerance, and metabolism will help us to identify critical habitat for optimum growth and survival.

The use of morphometric measurements to identify larval Pallid Sturgeon, from the closely related Shovelnose Sturgeon, has been an ongoing issue. Studies on morphological traits of larval *Scaphirhynchus* sturgeon have found small measurable differences within distinct populations (Snyder 2002; Kuhajda et al. 2007). However, in two different studies, Pallid Sturgeon from the upper Missouri River were found to be as genetically distinct from Pallid Sturgeon in the Atchafalaya River as Pallid Sturgeon were from Shovelnose Sturgeon (Campton et al. 2000; Tranah et al. 2001). Using microsatellite analysis, Schrey and Heist (2007) found that Pallid Sturgeon from the lower Missouri and Middle Mississippi rivers were genetically intermediate to those at the extremes (Schrey and Heist 2007). Additionally, hybridization between the two species has been identified in all Management Units (Schrey et al. 2011). Due to the abundance and accessibility of larval Shovelnose Sturgeon, many studies have used Shovelnose Sturgeon as a surrogate for Pallid Sturgeon. However, additional physiological information regarding specific requirements of larval *Scaphirhynchus* are needed.

Physiological Energetics of Larval Pallid Sturgeon

Physiological responses of fishes are driven to a large extent, by water temperature (Chipps and Wahl 2008). Water temperature regimes experienced by Pallid Sturgeon influence many physiological process such as timing of reproduction, spawning migration, gonadal development, embryo development, larval drift distance, growth, and

survival (Armour 1991; Keenlyn 1995; Kynard et al. 2002; USGS 2007; Braaten et al. 2008; DeLonay et al. 2009). Furthermore, bioenergetic models, which are widely used for estimating energy allocation and the metabolic demand of fishes, rely on water temperature as a primary driver affecting metabolic rates. Energy allocation in fishes can be partitioned into three basic components: metabolism, waste, and growth (Winberg 1956). Traditionally, bioenergetics models have been developed for juvenile and adult fish, but because rates are mass-specific, models are not easily extrapolated to larval fishes (Post 1990; Karjalainen et al. 1997). Additionally, larval fish bioenergetics models have received little application in management settings, owing to limited availability of data at these life stages (Post 1990). The development and corroboration of a larval Pallid Sturgeon energy budget would provide an important first step to modeling effects of environmental conditions on Pallid Sturgeon growth, survival and distribution.

Bioenergetic models can be used in a variety of ways to help answer management questions. They are commonly used to understand trophic structure and predator-prey dynamics within a system (e.g. European Anchovy *Engraulis encrasicolus* growth dependent on seasonal abundance of lower trophic level organisms (Politikos et al. 2011), seasonal trophic interactions of Bull Trout *Salvelinus confluentus* within a lake community (Beauchamp and Van Tassell 2001), and the impacts of Indo-Pacific lionfish *Pterois* spp. on native fish communities in the western North Atlantic Ocean, Caribbean Sea, and Gulf of Mexico (Cerino et al. 2013). Alternatively, bioenergetics models can be used to understand survival, mortality, and recruitment of larval fish. Small fish are more sensitive to environmental variation in temperature than large fish due to their higher, mass-specific metabolic rates (Post 1990). Understanding the energy requirements of

larval Pallid Sturgeon will help identify possible causes for larval mortality (Laurence 1969), allowing researchers to make more informed management decisions.

Research Objectives

To increase knowledge of habitat requirements for the growth of larval Pallid Sturgeon, I developed a bioenergetics model and tested the model against independent observations across a wide range of water temperatures and ration levels. The model will help inform managers of environmental requirements for the growth of larval Pallid Sturgeon. Moreover, when used in conjunction with a larval Pallid Sturgeon foraging model *(Deslauriers et al., unpublished)*, information on Pallid Sturgeon energetics can be used to assess and evaluate the usefulness of restored shallow water habitat as rearing habitat. Additionally, I highlight implications for model use and discuss potential limitations of the Modeling approach for evaluating growth dynamics.

To apply the model to a real-world setting, I used data collected from the upper and lower Missouri River to simulate growth of larval Pallid Sturgeon and compare differences in growth between time periods (pre- and post-dam construction). I also discuss the impacts of thermal suppression and serial discontinuity on Pallid Sturgeon survival and offer an alternative solution, through the use of selective withdrawal, to mitigate downstream effects on the native fish communities.

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CHAPTER 2. DEVELOPMENT OF A LARVAL PALLID STURGEON BIOENERGETICS MODEL

Abstract

Traditionally, bioenergetic models have been developed for juvenile and adult fish; however, these models are not easily extrapolated to larval fishes. To increase knowledge on the larval Pallid Sturgeon (*Scaphirhynchus albus*), the objective of this study was to develop a bioenergetics model to determine optimal temperature for growth of young-of-year Pallid Sturgeon. To develop this model, I estimated metabolic demands and growth over a range of temperatures and sizes. Pallid Sturgeon (0.005 to 9.094 g) were subjected to a range of temperatures commonly found in the Missouri River (13 – 28°C). Exogenously feeding larval fish were fed chironomids at *ad libitum* rations three times daily over multiple days to determine maximum consumption and estimate growth. I used static respirometry to quantify the routine respiration rate of larval Pallid Sturgeon. Using this model, I estimated daily consumption (g/d) for a 1-g fish, ranging from 0.15 g/d at 13°C to 0.31 g/d at 24°C. I also estimated daily oxygen consumption (M, g O_2/d) of a 1-g larval fish to range from 0.006 g O_2/d at 13°C to 0.016 g O_2/d at 28°C. To evaluate model performance, I constructed a biplot of observed versus predicted consumption rate and used regression analysis to determine similarity. The independent observations of daily consumption (g/d) fit the bioenergetic estimates of daily consumption ($F_{2,35}$= 477, R^2 = 0.96, P-Value < 0.001). The quantification of these bioenergetic parameters will allow us to estimate energetic requirements of larval Pallid Sturgeon, to make growth predictions from field observations, and to determine availability of optimal temperature ranges within the Missouri River.

Introduction

Dredging, channelization, and dam construction are some of the primary anthropogenic stressors that have altered habitat of Pallid Sturgeon *Scaphirhynchus albus* within their native range: the Missouri River and lower Mississippi River basins (Hesse and Mestl 1993; Galat et al. 1998). First described in 1905, little is known of the Pallid Sturgeon's early abundance and distribution (Pflieger et al. 1975); however, natural reproduction by Pallid Sturgeon is now believed to be negligible throughout much of the Missouri River system. As a result, reproduction is reduced or eliminated throughout the species range (Dryer and Sandvol 1993). Additional evidence of hybridization with the closely related Shovelnose Sturgeon *S. platorynchus* puts the Pallid Sturgeon at risk of genetic extinction through introgressive hybridization (55 Fed. Reg. 36641-36647; Dryer and Sandvol 1993; Rhymer and Simberrloff 1996; Schrey et al. 2011). This combination of evidence prompted the listing of Pallid Sturgeon under the Endangered Species Act in 1990 (55 Fed. Reg. 36641-36647).

Due to the critical status of the Pallid Sturgeon, short-term recovery efforts have focused primarily on artificial propagation and stocking of juvenile fish to increase the abundance of the species until factors affecting natural recruitment can be identified and mitigated (Committee 2005). Although much has been learned about propagation and rearing techniques, comparatively little is known about habitat suitability for larval Pallid Sturgeon (Bergman et al. 2008). Early life stages of the Pallid Sturgeon and the factors that affect their survival are poorly understood (Kallemeyn 1983). A few wild larvae have been identified in the Mississippi River (Hrabik et al. 2007) and the Yellowstone River (Braaten in litt., 2013); however, there is limited evidence of natural recruitment in

the Missouri River basin (USFWS 2014). Studies concentrating on this life stage have primarily focused on locating and identifying Pallid Sturgeon within the Missouri River (Keenlyn et al. 1994; Snyder 2002), understanding the habitat requirements and drift dynamics (Braaten et al. 2008; Phelps et al. 2010; Braaten et al. 2011; Phelps et al. 2012), and feeding and temperature as it relates to growth and survival (Kappenman et al. 2011; Kappenman et al. 2013).

Bioenergetic models are a widely used tool for estimating energy allocation and the metabolic demand of an organism. Energy allocation can be partitioned into three basic components: metabolism, waste, and growth (Winberg 1956). Temperature is considered the primary mechanism affecting the physiological rates of fishes (Chipps and Wahl 2008), and accordingly, is a major environmental input to the modeling approach. Estimating temperature effects on energy allocation will allow us to estimate the Pallid Sturgeon's timing of sexual maturity, spawning migration, gonadal development, embryo development, larval drift distance, growth, and survival – all of which are affected by water temperature (Armour 1991; Keenlyn 1995; Kynard et al. 2002; USGS 2007; Braaten et al. 2008; DeLonay et al. 2009). However, bioenergetic models have traditionally been developed for juvenile and adult fish and because rates are mass-specific, models are not easily extrapolated to larval fishes (Karjalainen et al. 1997). Therefore, it is vital to parameterize the larval Pallid Sturgeon bioenergetics model if we are to use this approach for evaluating factors affecting growth, survival and distribution of larvae.

Bioenergetics modeling has previously been used to evaluate food web connections and habitat suitability for sturgeon; these studies found that temperature and

prey availability were both important factors affecting growth rate of sturgeons (Bevelhimer 2002; Mayfield and Cech 2004; Niklitschek and Secor 2005). Understanding the physiological response of larval Pallid Sturgeon to environmental conditions would enhance habitat recovery efforts as well as rearing/stocking success. Assessing larval Pallid Sturgeon in the Missouri River has been difficult due to their near absence in the river and a lack of quantitative data. In this study, I developed a bioenergetics model for Pallid Sturgeon larvae and corroborate model output by testing it against independent observations across a range of temperatures. I discuss potential applications for model use and limitations of the model for evaluating growth dynamics.

Methods

Fish Husbandry

The larval Pallid Sturgeon used in this study were progeny from wild-caught adult females spawned under hatchery conditions at the USFWS at Gavin's Point National Fish Hatchery, Yankton, South Dakota. In 2013, 2 and 1 day post-hatch (dph) larvae were transported from the hatchery to the Fisheries Research Unit laboratory at South Dakota State University, Brookings, S.D. on June 14th and June 22nd, respectively. In 2014, 2 and 17 dph larvae were transported to the laboratory on June 17th and July 2nd, respectively.

Larvae were acclimated in 38 L aquaria (n = 30 per temperature, n = 90 total) at 13, 18, or 24 °C. Aquaria were connected to a recirculating system which pumped through a bag filter (X-100, Filter Specialists Inc., Michigan City, IN), a Carbon Basket Filter (CC50, Pentair Pool Products, Sanford, NC), and a U.V. Sterilizer (Emperor

Aquatics, Inc., Pottstown, PA). A digital temperature controller (NEMA 4X, Aqua Logic, Inc., San Diego, CA) was used to control water temperature within ± 1 °C of the target temperature. Water temperatures were recorded hourly in aquaria using submersible water temperature data loggers (Tidbit v2, Onset, Bourne, MA).

At onset of exogenous feeding (~ 18-19 mm), larvae were fed a mixture of dry food (70% Otohime and 30% Cyclopeeze (Kappenman et al. 2011) and thawed, chironomidae larvae. Dry food was removed from the diet once the fish measured 30 mm in total length. All fish were starved 24 h prior to the experimentation.

Model Development

The model developed here is structured after the popular Wisconsin bioenergetics model using the mass-balance equation,

$$C = (R + A + SDA) + (F + U) + G,$$

where consumption (C) is balanced by respiratory demands - standard metabolism (R), active metabolism (A) and specific dynamic action (SDA), waste losses - egestion (F) and excretion (U), and somatic growth (G) (Hanson et al. 1997). Consumption (C) and standard metabolism (R) are modeled as a function of body mass and water temperature (Hanson et al. 1997). Other parameters are expressed as a constant proportion of consumed energy (i.e., SDA, F and U) or as a fixed multiplier of standard metabolism (i.e., A; Winberg 1956). Additionally, information on temperature and weight-dependent maximum food consumption (C_{max}) is used to adjust consumption (C) to account for observed growth (i.e., p-value; Kitchell et al. 1977; Hanson et al. 1997).

Maximum Consumption

Maximum consumption (C_{max}) was measured at 13, 18, and 24 °C across a range of fish body sizes (n=38, 0.05 to 9.094 g, 21 to 155 mm). Due to the large range in body sizes, consumption trials were conducted in groups of 10, 3, or 1-fish depending on size category which I will describe as small, medium, and large, respectively, from this point forward. I observed high rates of mortality in small fish weighing less than 0.1 g; therefore, consumption trials consisted of 10 similar-sized fish sampled in a 1L container for three full days of feeding. Consumption trials using medium fish weighing 0.1-1.0 g were conducted in groups of 3 similar-sized fish in 1 L containers for five full days of feeding. Finally, consumption trials using large fish weighing more than 3.0 g were conducted using individual fish in 3 L containers for five full days of feeding.

For small fish feeding trials, a subset of 10 fish were weighed to the nearest 1.0 mg for average initial weight. A different subset of 10 fish were selected from the same pool for feeding experiments. Average end weights were measured using the remaining fish from each feeding trial. Medium and large fish feeding trials used the experimental fish for both initial and end weights, weighed to the nearest 1.0 mg.

All fish were fasted and left to acclimate for 24 h before initiation of feeding. Small fish trials lasted three days due to high mortality rates, whereas medium and large fish trials continued for five full days of feeding. During feeding days, fish were fed *ad libitum* rations (50% body weight) thawed chironomids three-times daily. Prior to feeding and following post-feeding removal, chironomids were blotted dry and weighed to the nearest 1.0 mg. To minimize error due to leaching, food that was not consumed was removed 30 minutes after each feeding. Chironomids were selected for use, due to their

predominance in the diets of larval and juvenile *Scaphirhynchus spp.* (Grohs et al. 2009), and the high selectivity exhibited by larval Pallid Sturgeon toward this prey over others (Rapp 2014). After feeding trials were complete, fish were fasted for 24-h then measured for body weight.

Food consumption (g/h) was calculated as the difference between the amount of food fed and that recovered from each aquaria. For fish in each aquaria, mean, hourly food consumption was determined from multiple measurements taken over a 3 to 5 day period. Mean hourly food consumption was multiplied by 24 to obtain a daily feeding rate estimate. Daily feeding rates were then divided by biomass of fish in each aquaria to obtain specific consumption estimates (g/g/d).

The relationship between body size and maximum food consumption was determined as,

$$C_{max} = aW^b \times f(t),$$

where C_{max} is the maximum consumption rate (g/g/d), W is fish mass (g), a and b are regression coefficients, and $f(t)$ is a temperature rate multiplier (Hanson et al. 1997).

Respiration

Respiration rates were quantified for larval Pallid Sturgeon (n=191, 0.01 to 5.7 g, 11.0 to 134.0 mm TL) at water temperatures ranging from 13- 28°C. Fiber optic oxygen probes that measured dissolved oxygen concentration in real time (NeoFox FOXY probes, Ocean Optics, Dunedin, FL) were outfitted to four static respirometers. Fish weighing 0.03 g or less were measured in groups of five fish in 15-30 mL respirometers, whereas larger fish were measured individually in 30 – 120 mL respirometers, depending

on fish size. In each trial oxygen concentration was measured in one respirometer without fish to correct for any microbial oxygen demand. Fish under 0.03 g were measured in groups of 5 fish whereas fish over 0.03 g were measured individually, increasing respirometer size as fish grew. Respiration trials were terminated after 60-90 minutes or if, oxygen concentration in the respirometers dropped below 5 mg/L.

Specific metabolism (M) for larval Pallid Sturgeon was calculated as

$$M, (\ g\ O_2/g\ fish/d) = \frac{(X \cdot V \cdot 1440)}{n},$$

where *X* is the rate of metabolism in g/L/min, *V* is the volume of the respirometer chamber minus the volume of the fish within the chamber (assuming a displacement of 1.0 ml water per g of fish (Chipps et al. 2009), and *n* is the number of fish in the chamber.

Using methods described in Tyler and Buldoc (2008), I optimized our respiration parameters to find the best fit for our respiration data. To do this, I began with the results of a multiple regression used to quantify the influence of body mass (B) and water temperature (T) on daily oxygen consumption (M) as,

$$M\ (g\ O_2/d) = x + bB + cT,$$

where x, b and c are regression coefficients. Using this equation, I estimated oxygen consumption for a 1.0 g fish at 28°C to estimate metabolism (g O_2/g/d) expressed as,

$$R = aW^b \times ACT \times f(t),$$

where R is resting metabolism (g O2/g/d) at optimal water temperature, W is fish mass in g of wet weight, a is the intercept value for a 1g fish, b is the weight dependent slope component, ACT is activity, and $f(t)$ is the temperature rate multiplier (Hanson et al. 1997). The values for intercept and slope were then compared with values obtained in similar bioenergetics models to determine a set an initial range for the optimization

technique. These values were refined using the R package 'nls2' which by systematically adjusting the values of four respiration parameters (RA, RB, RQ, and RTO; Hanson et al. 1997) by iteratively running the equation to determine the lowest residual sum of square value, thus finding the best fit to the data (Grothendieck 2013; R Core Team 2014).

Weight-Length Regression

To create an equation with which one could estimate weight from length, I regressed Log-transformed weight (g) against Log-transformed total length (mm; n=290, 0.05 to 30.1 g, 21 to 245 mm).

Model Validation

To validate the bioenergetics model, I compared model output with independent laboratory observations of feeding. To compare consumption rates, fish were fed *ad-libitum* rations for five day trials at 13, 18, or 24°C (n=27). The amount of food consumed was recorded using the same methodology as the feeding trials that were used to develop the model. To evaluate model performance, I constructed biplot of observed versus predicted consumption rate and used regression analysis to determine similarity.

Results

Maximum Consumption

Water temperature and body size influenced consumption rate and were used to predict daily consumption (C_{max}) as,

$$C_{max}\ (log_e\ g/d) = -2.632 + 0.681B + 0.0613T,$$

Where B is the natural logarithm of body mass ($\log_e$ g wet wt) and T is water temperature in degrees Celsius (multiple regression analysis, $F_{2,35} = 1752$, R^2=0.99, P<0.0001). Using this equation to estimate consumption (g/d) for a 1-g fish, I obtained values that ranged from 0.15 g/d at 13°C to 0.31 g/d at 24°C. The relationship between maximum food consumption C_{max} (g/g/d) and body mass (g) at 24°C was estimated as,

$$C_{max} = 0.313W^{-0.32},$$

(Table 1; Figure 1).

Respiration

Body size and water temperature were used to predict daily oxygen consumption (M) as,

$$M\ (log_e\ g\ O_2/d) = -6.570 + 0.831B + 0.068T,$$

(multiple regression analysis, $F_{2,188}$=9270, R^2=0.99, P<0.0001). Using these values, specific respiration rate (R, g/g/d), was estimated using an intercept value of 0.007 and a slope of -0.17 for a 1 g fish at 24°C. These values were used as a starting point for the optimization; for which I used an intercept range of 0.004 to 0.03 and a slope range of -0.04 to -0.3. The optimization technique found an RQ value of 1.98 and an RTO of 30, estimating specific rate of respiration (R, g/g/d) for a 1g fish at 30°C expressed as,

$$R = 0.017W^{-0.12},$$

where W is body mass in g wet weight (Table 1; Figure 2). Using this equation, I estimated daily oxygen consumption (M, g O_2/d) of a 1-g larval fish to range from 0.006 g O_2/d at 13°C to 0.016 g O_2/d at 28°C.

Weight-Length Regression

The Log-weight Log-total length linear regression model produced the equation

$$y = 0.367x + 1.865,$$

where x is Log-total length (mm) and y is Log-weight (g; Figure 3; $F_{1,288}$ = 31750, r2=0.991, p-value < 0.001).

Verification

The independent observations of daily consumption (g/d) fit the bioenergetic estimates of daily consumption ($F_{2,35}$= 477, R^2 = 0.96, P-Value < 0.001; Figure 4). Activity in sturgeon increases with increased water temperature (Mayfield and Cech 2004); therefore, I used information developed for Atlantic Sturgeon *Acipenser oxyrinchus* to model activity cost (Niklitschek and Secor 2005) and found the best activity fit for our data set. I adjusted ACT equal to 1 for simulations with temperatures ≤ 20°C, 1.5 for temperatures > 20°C.

Discussion

Evaluation of a bioenergetics model is the only method by which we can gain insights into model limitations (Hilborn and Mangel 1997) and is an important phase in the model development process (Chipps and Wahl 2008). Parameter estimates for metabolism closely resembled those of the juvenile Pallid Sturgeon Model (Chipps et al. 2009) and other larval fish (Post 1990; Karjalainen et al. 1997). The larval Pallid Sturgeon model estimates for the metabolic parameters Ma and Mb were 0.017 and -0.12, respectively (Table 1), compared to the estimates for the juvenile Pallid Sturgeon model

parameters Ma and Mb of 0.017 and -0.15 (Chipps et al. 2009). Model estimates for the consumption intercept parameter, Ca, varied between the larval Pallid Sturgeon (0.313) and the juvenile Pallid Sturgeon model (0.552); however, the slope parameter, Cb, remained the same between models (-0.32; Chipps et al. 2009). Additionally, parameter estimates for consumption performed well in the biplot regression analysis (Figure 4). Therefore, I can conclude that both the larval Pallid Sturgeon metabolic and consumption parameter estimates are reasonable and comparable to the independently derived bioenergetics model for Juvenile Pallid Sturgeon.

Model estimates are also comparable to other larval fish. At optimal temperatures, the young-of-year Yellow Perch *Perca flavescens* bioenergetics model estimates metabolic parameter values for Ma and Mb of 0.035 and -0.20, respectively, and model estimates consumption parameter values for Ca and Cb of 0.051 and -0.42 (Post 1990). Additionally, the young-of-year Eurasian Perch *Perca fluviatilus* metabolic parameter estimates for Ma and Mb were 0.0108 and -0.20, respectively, and model estimates consumption parameter values for Ca and Cb of 0.51 and -0.42 (Karjalainen et al. 1997). These two species are closely related, explaining the close degree of similarity between perch models; however, examining these models provides a general range to compare with the more distantly related young-of-year Pallid Sturgeon model estimates.

A corroborated bioenergetics model can be versatile in its many applications. In particular, the larval Pallid Sturgeon bioenergetics model could be used for assessing fish growth in areas of recovered shallow water habitat or evaluating the impact of thermal suppression from deep-release storage reservoirs. In the 2003 U.S. Fish and Wildlife Service Amended Biological Opinion, the U.S. Army Corps of Engineers was mandated

to restore 1,200 additional acres of shallow water habitat for the larval Pallid Sturgeon (USFWS 2003). Shallow water habitat restoration is a costly rehabilitation technique, and up until now, has had little to no method of determining its contribution to Pallid Sturgeon recovery. At the onset of first feeding, lipids provide energy for swimming activity (Kamler 2008). Based on drift velocity and time to settling, models suggests that larval Pallid Sturgeon have a drift distance ranging from of 245 to 530 km (Kynard et al. 2007; Braaten et al. 2008; Braaten et al. 2011). Therefore, we have the ability to, and need to, understand prey-availability in the stretches of river Pallid Sturgeon larvae are settling to assess survival at ontogeny. Alternatively, cold-water releases downstream of reservoirs have been shown to negatively affect aquatic communities (Sherman et al. 2007). In reservoir tailrace reaches, such as the first 110 km below Garrison Dam, average midsummer temperatures have been reduced by up to 10°C from the historic average (see Chapter 3). Serial discontinuity in river temperatures has been well-documented (Ward and Stanford 1983) and may be of serious concern within the Missouri River. With the collection of field data on environmental conditions, the bioenergetics model will make it possible to assess the quantity of readily available quality habitat for larval Pallid Sturgeon growth in the Missouri River basin.

One drawback of this study is that all experimental sturgeon were progeny of the Great Plains Management Unit (GPMU; USFWS 2014). Predictability of growth rates in southern fishes differ, due to differences in food consumption and metabolic rate at higher temperatures (Meyer 2011). Additionally, southern Pallid Sturgeon have been found to be as genetically distinct from northern Pallid Sturgeon as Pallid Sturgeon are from Shovelnose Sturgeon (Schrey and Heist 2007), creating additional possibility in

error when applying this model to the lower Mississippi River fish. Future research would be to assess the degree of difference in Northern versus Southern genetic strains of Pallid Sturgeon in order to adjust model parameters as necessary.

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Tables and Figures

Table 1. Equations and parameters used to parameterize the larval Pallid Sturgeon bioenergetics model. Symbols and adjoining descriptions are described in detail in Hanson et al. (1997). W represents wet weight of fish in g. For the temperature rate multiplier, the parameters V, X, Z, and Y are fitted with CQ, CTM, and CTO (as shown) or with RQ, RTM, and RTO.

Symbol	Description	Value
	Consumption: C = $P_{Cmax} \cdot aW^b \cdot f(T)$	
P_{Cmax}	Proportion of maximum consumption ($C_{max}=aW^b$)	Fitted parameter
a	Intercept for W dependence of C_{max}	0.313
b	Slope for W dependence of C_{max}	-0.32
CQ	Q_{10} rate at low temperatures	1.85
CTO	Optimum feeding temperature	24
CTM	Maximum feeding temperature	30
	Metabolism: R= $aW^b \cdot f(T) \cdot$ACT	
a	Intercept for W dependence of R	0.017
b	Slope for W dependence of R	-0.12
RQ	Q_{10} rate at low temperatures	2.07
RTO	Optimum temperature for respiration	30
RTM	Maximum (lethal) water temperature	35
ACT	Activity multiplier, ≤ 20°C	1.0
	Activity multiplier, > 20°C	1.5
	Energy losses: F=FA · C; U=UA · (C-F); S=SDA· (C-F)	
FA	Proportion of energy egested (F)	0.1[a]
UA	Proportion of energy excreted (U)	0.04[a]
SDA	Specific dynamic action (S)	0.13[a]
	Temperature rate multiplier $f(T) = (V^x e^{(x(1-V))})$	
(T)	Observed water temperature (°C)	
(V)	(CTM-T)/(CTM-CTO)	
(X)	$(Z^2(1+(1+40/Y)^{0.5})^2)/400$	
(Z)	Log_e(CQ)(CTM-CTO)	
(Y)	Log_e(CQ)(CTM-CTO+2)	

[a] From (Niklitschek 2001).

Table 2. Temperature-dependent consumption estimates for larval Pallid Sturgeon fed *ad libitum* rations of chironomids. Values in parenthesis represent 1 SE.

Water Temperature (°C)	**N**	**Mean fish mass (g)**	**Mean daily consumption (g/d)**	**Mean specific consumption (g/g/d)**
13	15	2.05 (0.63)	0.224 (0.060)	0.316 (0.058)
18	11	2.25 (0.63)	0.305 (0.074)	0.440 (0.134)
24	12	2.95 (0.89)	0.488 (0.121)	0.746 (0.224)

Table 3. Temperature-dependent metabolic estimates for larval Pallid Sturgeon in static respirometers. Values in parenthesis represent 1 SE.

Water Temperature (°C)	**N**	**Mean fish mass (g)**	**Mean daily metabolism (g O2/d)**	**Mean specific metabolism (g O2/g/d)**
13	25	0.40 (0.22)	0.0045 (0.0031)	0.0015 (0.0007)
15	18	1.68 (0.43)	0.0241 (0.0089)	0.0068 (0.0019)
18	62	0.17 (0.04)	0.0006 (0.0002)	0.0011 (0.0002)
21	14	0.06 (0.01)	0.0001 (0.00004)	0.0010 (0.0003)
24	48	0.75 (0.21)	0.0099 (0.0036)	0.0040 (0.0008)
28	24	0.02 (0.001)	0.00001 (0.000001)	0.0004 (0.00003)

Figure 1. The specific rate of consumption, in grams of food per gram of fish (wet weight) per day, plotted across the range of likely temperatures Pallid Sturgeon larvae may encounter within the Missouri River basin.

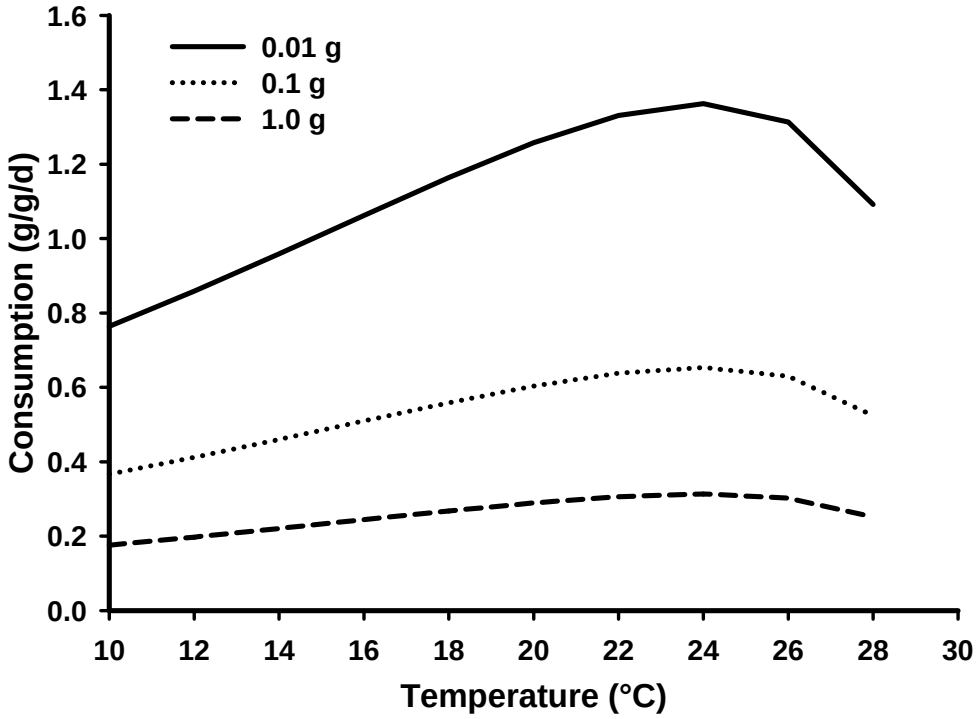


Figure 2. The specific rate of metabolism, in grams of oxygen per gram of fish (wet weight) per day, plotted across the range of likely temperatures Pallid Sturgeon larvae may encounter within the Missouri River basin.

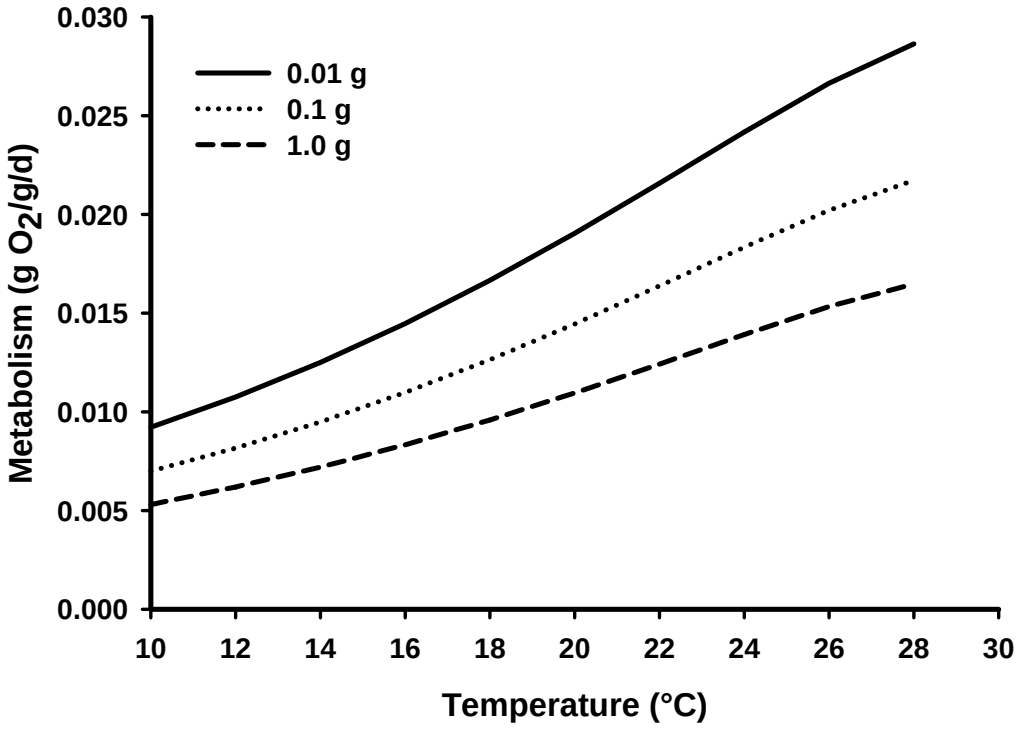


Figure 3. Log weight to log total length linear regression model (n=290; $F_{1,288}$ = 31750, r^2=0.991, p-value < 0.001). Dashed line represents linear regression equation y=0.367x+1.865.

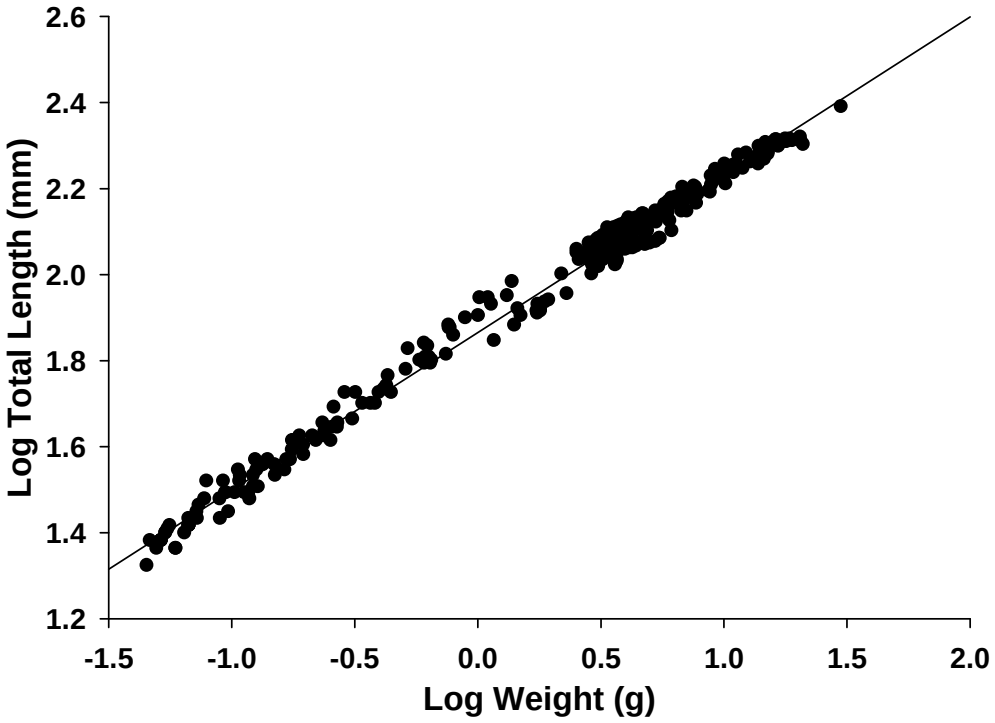
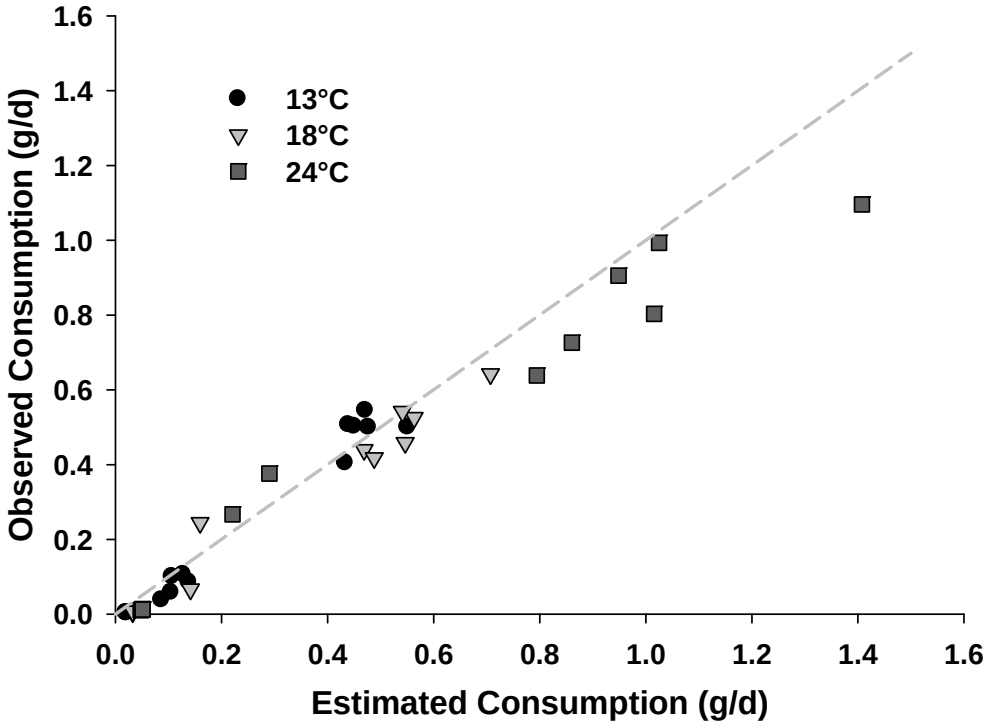


Figure 4. The bioenergetics model predicted values of daily consumption (g/d) plotted against independent observations of daily consumption at 13, 18, or 24°C ($F_{2,35} = 477$, $r^2 = 0.96$; P-Value < 0.001). Dashed line represents 1:1 relationship.



CHAPTER 3. APPLICATION OF THE LARVAL PALLID STURGEON BIOENERGETICS MODEL

Abstract

Cold-water releases below large dams can have an important influence on fisheries productivity. In the upper Missouri River, the construction of large impoundments has been associated with changes in water temperature regimes, seasonal hydrographs, water turbidity, and migration corridors for fishes. Habitat alterations in the Missouri River are believed to contribute to recruitment failure in the federally endangered Pallid Sturgeon (*Scaphirhynchus albus*), with research priorities focused on the larval stage of the species. Using a bioenergetics approach, I simulate growth dynamics of larval Pallid Sturgeon in the upper and lower Missouri River. Long-term water temperature data were obtained below Garrison Dam (Bismarck, ND) during pre-dam (1932-1952) and post-dam (1960-2001) periods; data for similar time periods were obtained from the lower Missouri River (LMR) near Boonville Missouri. In the Spawning Scenario, simulating larval growth over a growing season starting from hatch and feeding at 50 % maximum consumption, I found a 1.0 % increase and a 65.2 % decrease in end weights from the Pre-Dam to the mean Post-Dam time periods in the LMR and GR, respectively. I also found 4.1 % and 38.3 % fewer number of days and 5.0 % and 53.6 % fewer cumulative thermal units (CTU) in the LMR and GR, respectively. In the Stocking Scenario, simulating larval growth over a growing season starting from a stocking on July 1st and feeding at 50 % maximum consumption, I found a 7.5 % increase and 37.4 % decrease in end weights from the Pre-Dam to mean Post-Dam

time periods in the LMR and GR. This simulation also resulted in a 1.1 % more and 24.1 % fewer CTU in the LMR and GR. My findings suggest that the cold waters of the deep-release storage reservoirs are negatively impacting the growth potential of larval Pallid Sturgeon within at least 110 km downstream proximity of Garrison Dam; however, at approximately 1880 km below impoundment, the negative impacts from temperature are no longer detected. With six major dams along the main stem upper Missouri River, thermal impacts may be a leading cause of recruitment failure in Pallid Sturgeon and I recommend additional research. Supplementary temperature data should be collected to determine how far reaching the thermal impacts are negatively affecting age-0 Pallid Sturgeon survivorship. Additionally, I recommend the use of field studies to test and verify simulation results.

Introduction

A wide range of thermal environments were naturally available within the Missouri and lower Mississippi River basins (Jacobson and Galat 2006), the native range of the federally endangered Pallid Sturgeon *Scaphirhynchus albus* (Keenlyne 1989). Historically, the large hydrologic variation existing in the Missouri River offered a wide variety of physical habitats to migrating sturgeon (DeLonay et al. 2009). Snow-melt hydrology from the Rocky Mountains and Great Plains mixed with the runoff from frontal storms and tropical air masses from the Gulf of Mexico, leading to a characteristic double-peaked annual hydrograph with March and May-June flood pulses (DeLonay et al. 2009). These effects have been known to trigger critical behaviors (e.g., spawning and migration) that significantly affect Pallid Sturgeon reproductive success (Wildhaber et al. 2011a). However, within the past century, the hydrograph of the Missouri River has been altered primarily as a result of the construction of six deep-release storage dams (Keenlyne 1989; USFWS 2000).

Water temperature is an important cue for spawning migration (DeLonay et al. 2009) and embryonic development rate (Kamler 2008). It has also been linked to larval *Scaphirhynchus* spp. drift distance, growth, and survival (Armour 1991; Keenlyn 1995; Kynard et al. 2002; USGS 2007; Braaten et al. 2008). Additionally, alterations in the natural temperature regime affect recruitment success (Fry 1971; Koehn 2001). Throughout much of the Missouri River system, natural reproduction by Pallid Sturgeon is believed to be negligible. Early life stages of the Pallid Sturgeon and the factors that affect their survival are poorly understood (Kallemeyn 1983) but habitat quality is likely a contributing factor (DeLonay et al. 2009). Although much has been learned about

propagation and rearing techniques, comparatively little is known about habitat suitability for larval Pallid Sturgeon (Bergman et al. 2008). Historically, the Missouri River was characterized by a wide, shifting, braided channel with abundant sandbars and woody debris (Wildhaber et al. 2011b). Much of this changed through dredging, channelization, and construction of the main stem dams. In particular, the loss of historical shallow water habitat has been singled out as a primary reason for the decline of the Pallid Sturgeon (USFWS 2000). In response to this finding, a range-wide stocking program was implemented (USFWS 2008) and the U. S. Army Corps of Engineers (USACE) was mandated to restore 20,000 acres of shallow water habitat (USFWS 2000). Shallow water habitat is described as areas of warm, shallow and turbid habitat with braided channels and large sandbars, measuring less than 1.5 m deep and slow water velocities of less than 0.6 m/s on average (Gosch et al. 2013). USACE has been actively creating shallow water habitat by creating off-channel habitats, such as chutes and backwaters, and modifying or removing existing control structures (Gosch et al. 2013); however, it is unclear whether restoring shallow water habitat alone will provide adequate quality habitat to rebound the population.

Cold water release from large, deep reservoirs has been shown to negatively affect downstream communities (Sherman et al. 2007). Annual water temperatures in the Missouri River have changed significantly below Garrison Dam since it was closed 1953 (Figure 1). Seasonal water temperatures have shifted to a cooler, delayed spring, cooler summer, and protracted, warmer water temperatures into autumn. Mid-summer temperatures averaged ten degrees lower after impoundment than historical temperatures. Further down river, in Boonville, Missouri, a similar change in temperature is not evident

(Figure 2). To explore how historical changes in water temperature might influence growth of age-0 Pallid Sturgeon, I used a larval Pallid Sturgeon bioenergetics model to compare growth trajectories under historical and contemporary river water temperatures. I highlight implications of water temperature for growth of larval sturgeon and potential limitations on survival.

Methods

Data Collection

The influence of water temperature on growth rate of larval Pallid Sturgeon was evaluated using a bioenergetics model (see Chapter 2). Growth simulations were performed using long-term water temperature data collected from two locations, varying in latitude and downstream proximity to a main stem dam. The Lower Missouri River Reach (LMR) data set was collected from the Boonville, Missouri water treatment plant from 1938-2009, approximately 960 kilometers below Gavin's Point Dam at 38°58'25.10" N and 92°44'35.67" W. The Garrison Reach (GR) data set was collected from the Bismarck, North Dakota water treatment plant logbooks from 1932-2001, approximately 110 kilometers below Garrison Dam at 46°48'29.98" N and 100°47'01.46" W. Water temperature data were grouped into three 20-y time periods: Pre-Dam (1932-1952 in Bismarck, 1938-1952 in Boonville), Early Post-Dam (1960-1980), and Recent Post-Dam (1981-2001). This was done by averaging daily temperature across the time period. The Pre- and Post-Dam time periods are based on the opening of Garrison dam in 1953. The same time periods were used for the LMR and GR simulations, with the exception of six years of missing data in the Pre-Dam time period.

The LMR data set did not show much variability between time periods, so I accepted the Pre-Dam average without data from 1932-1937.

Data spanning almost a century is rare, and thus the occasional missing data point (each data point representing one day) is to be expected. Four rules were applied to account for missing values within each data set: (1) for a single missing value, the preceding and succeeding value were averaged, (2) for two consecutive missing values, the two preceding the first value were averaged to replace the first missing value and the two succeeding the second value were averaged to replace the second missing value, (3) for three consecutive missing values, step two was used for the first and last missing value while the middle values were averaged using the new first and last values, (4) no values were averaged for four or more consecutive missing values, unless the data preceding and succeeding were the same.

Simulated effects of temperature on spawning and larval growth

To simulate an entire growing season for a Pallid Sturgeon hatched in each of the two segments of river, hereafter referred to as the *spawning scenario simulation*, I estimated time of spawning, hatching, first feeding, and end of growing season based on temperature-dependent development rates. In the upper Missouri River, Pallid Sturgeon generally spawn between 17 and 23°C (P. Braaten, USGS, Ft Peck MT, *personal communication*). To simulate spawning and embryo incubation, I used the first day with average daily temperature at or above 17 °C as the simulated spawning date. Hatching date and date of first feeding were then estimated from cumulative thermal units (CTUs). Following fertilization, hatching occurred after 200 CTUs were accumulated; first

feeding occurs at about 20 mm in length or after about 400 CTUs post- fertilization (Kynard et al. 2007; Kappenman et al. 2013). Thus, first feeding was approximated at 400 CTU past spawning and marks the initiation of our simulation. All simulations were run with a starting wet weight of 0.01 g and a fixed feeding rate of 10, 50, or 100% maximum consumption (equivalent to a p-value of 0.1, 0.5 or 1.0, respectively; Hanson et al. 1997). Predator energy densities were measured using bomb calorimetry on endogenous larvae and estimated as 2736 J/g. The prey energy density estimate was taken from James et al. (2012), who estimated chironomidae energy density as 2922 J/g in South Dakota. The simulation period ended (i.e., day) when mean, daily water temperature was below 13 °C for five consecutive days. At 13°C, feeding and growth rates of larval Pallid Sturgeon significantly decline (see Chapter 2).

Simulated effects of temperature on stocked larval growth

To simulate an entire growing season for a Pallid Sturgeon hatched in each of the two segments of river, hereafter referred to as the *stocking scenario simulation*, I estimated the growth of a larval Pallid Sturgeon, if stocked on July 1st, and end of growing season at 13°C. In 2013 and 2014, Pallid Sturgeon hatched between mid-June and early July (see Chapter 2), therefore I selected July 1st as a starting point to simulate first-feeding larvae from the mid-June hatch. All simulations ran with a starting mass of 0.01g, a fixed feeding rate of 10, 50, or 100% maximum consumption (equivalent to a p-value of 0.1, 0.5 or 1.0, respectively; Hanson et al. 1997), and the same energy densities as the previous simulation.

To evaluate the influence of water temperature on growth, I calculated the percent difference in mean ending weight of age-0 Pallid Sturgeon between pre- and post-dam conditions of each river reach (GR) and (LMR) using the equation

$$\frac{x - y}{y},$$

where x represents the mean post-dam values and y represents pre-dam values.

Results

Simulated effects of temperature on spawning and larval growth

Lower Missouri River (LMR) simulated end weights at 10 % maximum consumption were 0.011 g, 0.015 g, and 0.012 g for the Pre-Dam, Early Post-Dam, and Recent Post-Dam time periods, respectively. This simulation resulted in a 22.7 % decrease in end weight from the Pre-Dam to the mean Post-Dam time periods. Simulated end weights at 50 % maximum consumption were 2.94 g, 3.05 g, and 2.89 g for the Pre-Dam, Early Post-Dam, and Recent Post-Dam time periods, respectively. This simulation resulted in a 1.0 % decrease in end weight from the Pre-Dam to the mean Post-Dam time periods. Simulated end weights at 100 % maximum consumption were 203.72 g, 209.10 g, and 196.67 g for the Pre-Dam, Early Post-Dam, and Recent Post-Dam time periods, respectively. This simulation resulted in a 0.4 % increase in end weight from the Pre-Dam to the mean Post-Dam time periods. Additionally, there were 4.1 % fewer days and 5.0 % fewer cumulative thermal units (CTU) from the Pre-Dam to the mean Post-Dam time periods (Table 1).

Simulated end weights for the Garrison Reach (GR) at 10 % maximum consumption were 0.014 g, 0.019 g, and 0.019 g for the Pre-Dam, Early Post-Dam, and

Recent Post-Dam time periods, respectively. This resulted in a 35.7 % increase in end weight from the Pre-Dam to the mean Post-Dam time periods. Simulated end weights at 50% maximum consumption were 2.64 g, 0.89 g, and 0.95 g for the Pre-Dam, Early Post-Dam, and Recent Post-Dam time periods, respectively. This resulted in a 65.2 % decrease in end weight from the Pre-Dam to the mean Post-Dam time periods. Simulated end weights at 100% maximum consumption were 120.71 g, 29.82 g, and 32.48 g for the Pre-Dam, Early Post-Dam, and Recent Post-Dam time periods, respectively. This resulted in a 74.2 % decrease in end weight from the Pre-Dam to the mean Post-Dam time periods. Additionally, there were 38.3 % fewer in days and 53.6 % fewer cumulative thermal units (CTU) from the Pre-Dam to the mean Post-Dam time periods (Table 1).

Simulated effects of temperature on stocked larval growth

Simulated end weights for the Lower Missouri River Reach (LMR) at 10 % maximum consumption were 0.0062 g, 0.0103 g, and 0.0062 g for the Pre-Dam, Early Post-Dam, and Recent Post-Dam time periods, respectively. This resulted in a 33.1 % increase in end weight from the Pre-Dam to the mean Post-Dam time periods. Simulated end weights at 50 % maximum consumption were 2.12 g, 2.35 g, and 2.21 g for the Pre-Dam, Early Post-Dam, and Recent Post-Dam time periods, respectively. This resulted in a 7.5 % increase in end weight from the Pre-Dam to the mean Post-Dam time periods. Simulated end weights at 100 % maximum consumption were 69.30 g, 82.65 g, and 72.15 g for the Pre-Dam, Early Post-Dam, and Recent Post-Dam time periods, respectively. This resulted in an 11.7 % increase in end weight from the Pre-Dam to the mean Post-Dam time periods. The number of days remained the same for all three time-

periods and there were 1.1 % fewer CTU from Pre-Dam to the mean Post-Dam time periods.

Garrison Reach simulated end weights at 10 % maximum consumption were 0.013 g, 0.021 g, and 0.021 g for the Pre-Dam, Early Post-Dam, and Recent Post-Dam time periods, respectively. This resulted in a 61.5 % increase in end weight from the Pre-Dam to the mean Post-Dam time periods. Simulated end weights at 50 % maximum consumption were 2.43 g, 1.51 g, and 1.53 g for the Pre-Dam, Early Post-Dam, and Recent Post-Dam time periods, respectively. This resulted in a 37.4 % decrease in end weight from the Pre-Dam to the mean Post-Dam time periods. Simulated end weights at 100 % maximum consumption were 89.84 g, 72.28 g, and 72.64 g for the Pre-Dam, Early Post-Dam, and Recent Post-Dam time periods, respectively. This simulation resulted in a 19.3 % decrease in end weight from the Pre-Dam to the mean Post-Dam time periods. The number of days remained the same for all three time-periods and there were 24 % fewer CTU from Pre-Dam to the mean Post-Dam time periods.

Discussion

My findings show that the cold water releases of large reservoirs can negatively impact the growth potential of larval Pallid Sturgeon within at least 110 km downstream proximity. Within the GR, thermal differences pre- and post-dam construction resulted in dramatic differences in end weight for both Spawning and Stocking Scenarios (Figures 4 & 6). In the GR, the highest end weights, occurring in the 50 % and 100 % feeding rate scenarios, were associated with the Pre-Dam time period, which had the both most cumulative thermal units (CTU) and the most number of days (Table 1). In both the

LMR and GR, simulations with large increases in end weight from the Pre-Dam to Post-Dam time periods occurred in the 10 % feeding rate scenarios. In each of these scenarios, the low feeding rate caused weights to decrease from the initial starting weight. In time periods with cooler temperatures, lower metabolic costs supported the highest end weights.

At the LMR, 960 km below the nearest impoundment and 1880 km below Garrison Dam, the negative impacts from temperature are no longer detected and variation in end weight can be attributed to natural fluctuations in temperature. The LMR is nearly 9 times further from the closest upstream reservoir than the GR, accounting for the lower differences in thermal suppression, as seen in the GR. The LMR maintained relatively consistent temperatures throughout all three time periods resulting in negligible differences in end weights at 50 % and 100 % feeding rates (Figures 3 & 5).

These results are consistent with the findings of similar studies. Post-closure of the Glen Canyon Dam in 1963 on the Colorado River, the mid-summer temperature dropped around 10 °C causing behavioral changes and mortality in larval Colorado Squawfish *Ptychocheilus Lucius* (Clarkson and Childs 2000). Following closure of the Flaming Gorge Dam in 1962 in the Green River, Utah, several species (Roundtail Chub *Gila robusta*, Speckled Dace *Rhinichthys osculus*, etc.) disappeared from the uppermost portions of the 104 km tailwater reach (Vanicek and Franklin 1970). A model developed to predict the population response of Murray Cod *Maccullochella peellii peelii* and Trout Cod *M. macquariensis,* following the introduction of cold water, predicted reductions of up to 90 % in the abundance of female fish and were consistent with the observed local extinction of these species in the Mitta Mitta River (Todd et al. 2005). A range of other

studies have documented the negative effects physiological effects of thermal suppression on fish (Astles et al. 2000; Clarkson and Childs 2000; Ryan et al. 2002; Todd et al. 2005) including impeding gonadal maturation, spawning (Holden and Stalnaker 1975) and embryonic development of fish (Marsh 1985).

Thermal serial discontinuity within a system affects fish assemblages and native fish success (Koehn 2001). Assuming thermal affects to be similar among all six major dams along the main stem upper Missouri River, reduced water temperatures may be an important factor regarding recruitment failure in Pallid Sturgeon due to the likelihood of higher mortality rates in slower growing larval fish (Post and Prankevicius 1987; Rice et al. 1987; Meekan and Fortier 1996). In comparison, cold water release from dams in southeastern Australia are estimated to affect hundreds of kilometers of river downstream (Sherman et al. 2007). Restoring the hydrograph on intensively engineered rivers, such as the Missouri River, may restore important flow-related factors including water temperature (Jacobson and Galat 2006). To accomplish this, selective withdrawal practices are commonly used but widely thought of as a costly renovation including a multiple-outlet structure to provide the selective withdrawal capability (Phillips 2001). However, the cost of such structures may be mitigated by modifying the outlet structure to access to surface-layer water, using pumps to move surface layer water into withdrawal layers, and using curtains upstream to block downstream movement of cold water (Sherman 2000). Sherman (2007) modeled the outcome of the alternative method using near-surface water to mitigate the cold waters and estimated temperature increases of 4 to 6 °C during the crucial spring-early summer post-spawning period (Sherman et al.

2007) which would significantly increase larval fish growth potential in the tailrace reach.

What is still unknown at this time is the distance downstream from a reservoir that thermal suppression negatively affects the growth potential of Pallid Sturgeon. The geographic extent of thermal suppression is dependent on discharge rate, river flowing depth and local climate (Sherman et al. 2007). It is also unknown to what extent restored areas of shallow water habitat are negatively affected by the cold waters rendering the areas useless to newly hatched larval Pallid Sturgeon. I recommend the construction of additional models to determine the range of negative effects from thermal suppression and the cost and efficiency of renovating Missouri River dams.

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Tables and Figures

Table 1. Growing season information including length of growing season in cumulative thermal units (CTU) and days, mean water temperature including standard error, and maximum water temperature. The three time periods represented are pre-dam construction from 1932-1952, early post-dam construction 1960-1980, and recent post-dam construction 1981-2001.

	Growing Season (CTU)	Growing Season (days)	Mean Water Temperature (°C)	Maximum Water Temperature (°C)
Simulated Spawning Scenario				
Lower Missouri River Reach				
Pre-dam	3618	158	23 (0.31)	27
Early post-dam	3416	150	23 (0.39)	27
Recent post-dam	3455	153	22 (0.38)	27
Garrison Reach				
Pre-dam	2216	107	21 (0.34)	24
Early post-dam	1011	65	15 (0.49)	17
Recent post-dam	1047	67	15 (0.48)	17
Simulated Stocking Scenario				
Lower Missouri River Reach				
Pre-dam	2323	92	21 (0.33)	24
Early post-dam	2294	92	16 (0.11)	17
Recent post-dam	2300	92	16 (0.10)	17
Garrison Reach				
Pre-dam	1952	92	25 (0.52)	27
Early post-dam	1483	92	25 (0.52)	27
Recent post-dam	1482	92	25 (0.52)	27

Figure 1. Mean daily water temperatures in the Missouri River below Garrison Dam, ND. Time periods represent three, 20-year intervals based on pre-dam (1932-1952), early post-dam (1960-1980) and recent post-dam (1981-2001) periods associated with the closing of Garrison Dam. Data were collected from the water treatment plant in Bismarck, North Dakota (http://www.bismarck.org/index.aspx?NID=216).

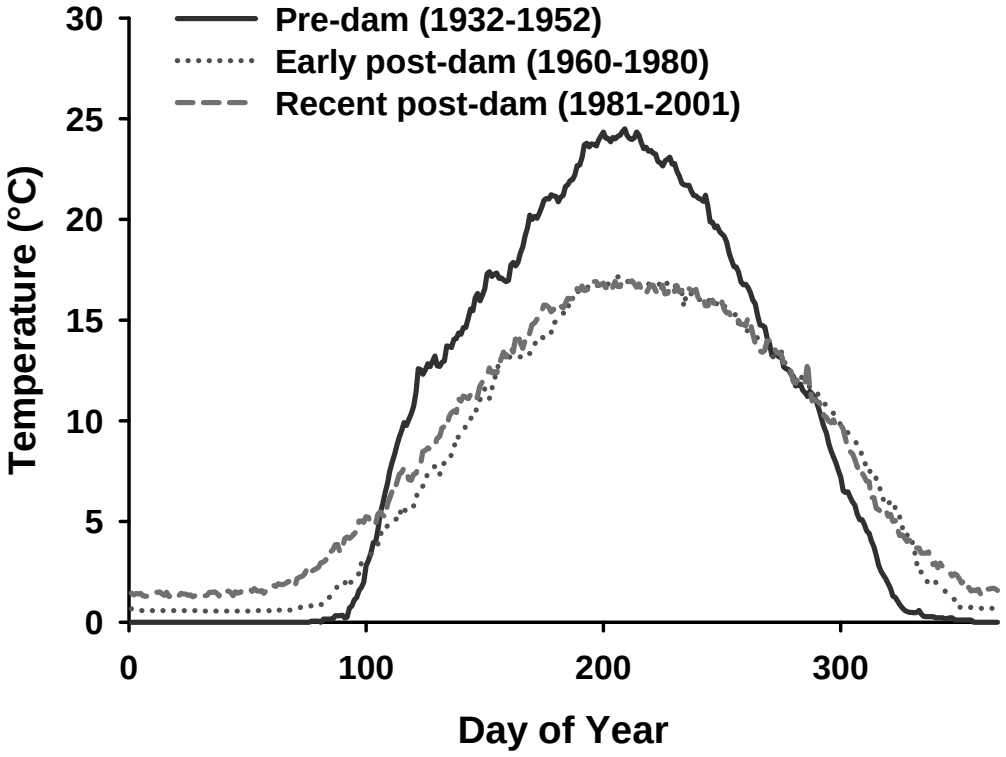


Figure 2. Mean daily water temperatures in the lower Missouri River near Boonville, MO. Time periods represent three, 20-year intervals based on pre-dam (1932-1952), early post-dam (1960-1980) and recent post-dam (1981-2001) periods corresponding with the closing of Garrison Dam, ND. Data were collected from the water treatment plant in Boonville, Missouri (http://www.boonvillemo.org/Water.aspx).

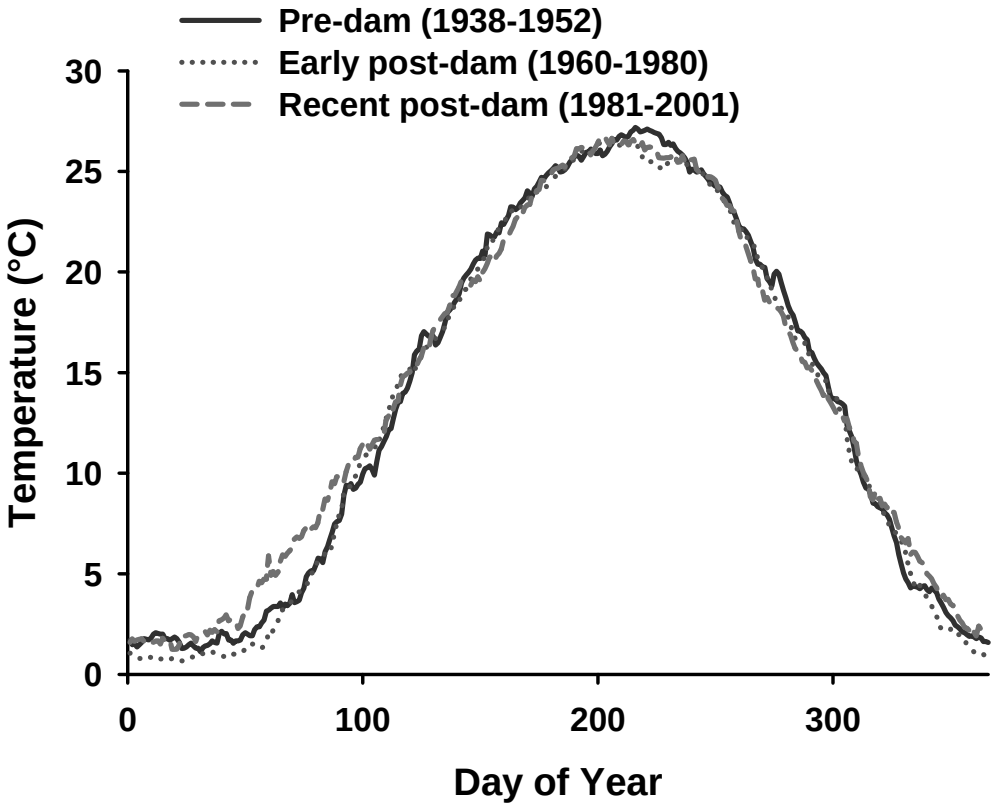


Figure 3. Spawning simulation scenario showing the weight accumulation throughout the three time periods in the Lower Missouri River Reach (LMR). Graphs are in increasing order of feeding rates with p-values correlating to the proportion of maximum consumption, where p = 1 is equivalent to feeding at 100% maximum consumption.

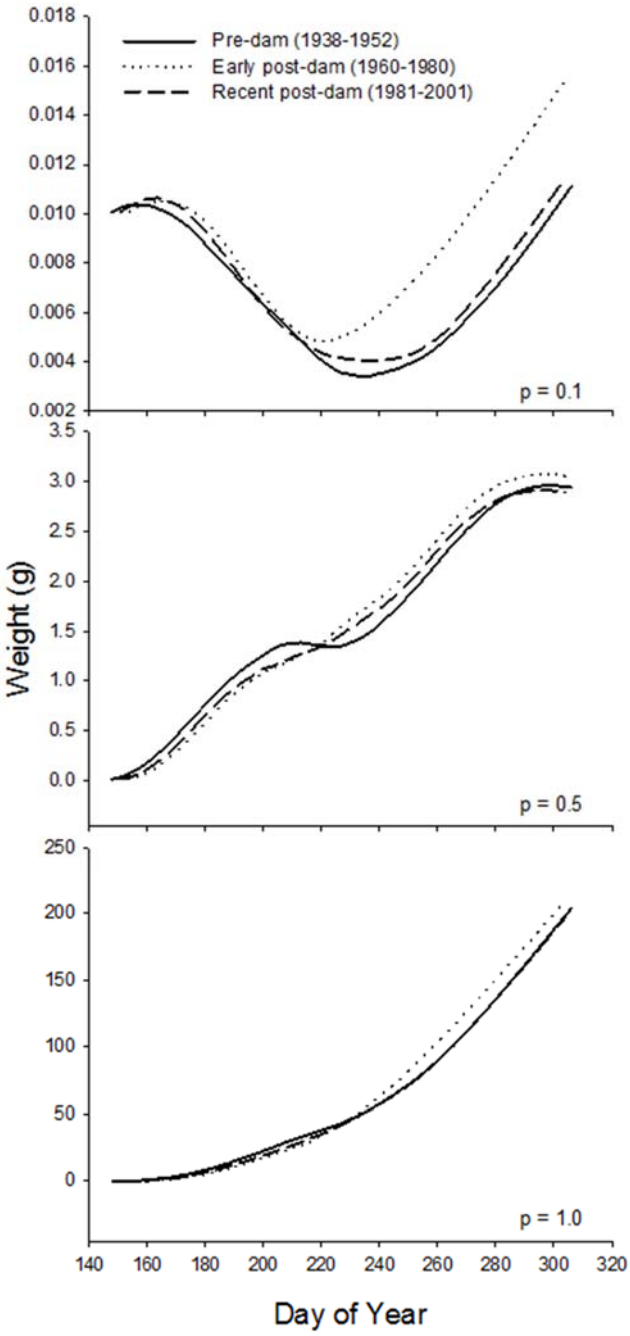


Figure 4. Spawning simulation scenario showing the weight accumulation throughout the three time periods in the Garrison Reach (GR). Graphs are in increasing order of feeding rates with p-values correlating to the proportion of maximum consumption, where p = 1 is equivalent to feeding at 100% consumption rate.

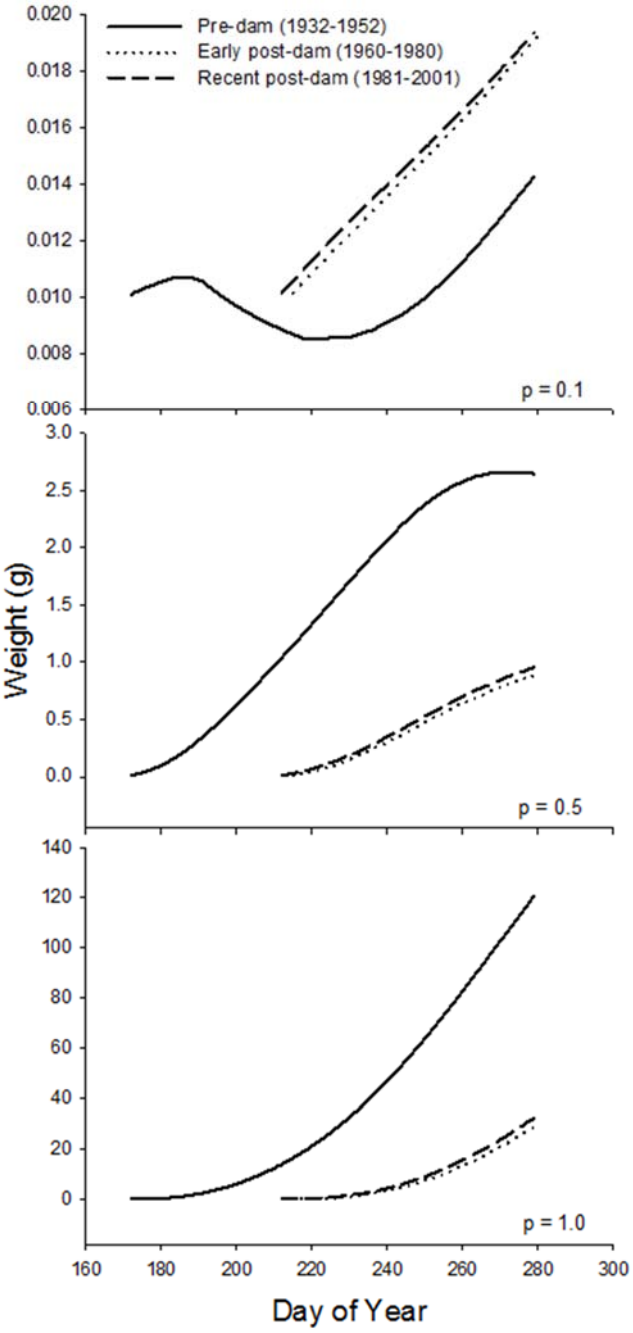


Figure 5. Stocked simulation scenario showing the weight accumulation throughout the three time periods in the Lower Missouri River Reach (LMR). Graphs are in increasing order of feeding rates with p-values correlating to the proportion of maximum consumption where p = 1 is equivalent to feeding at 100% consumption rate.

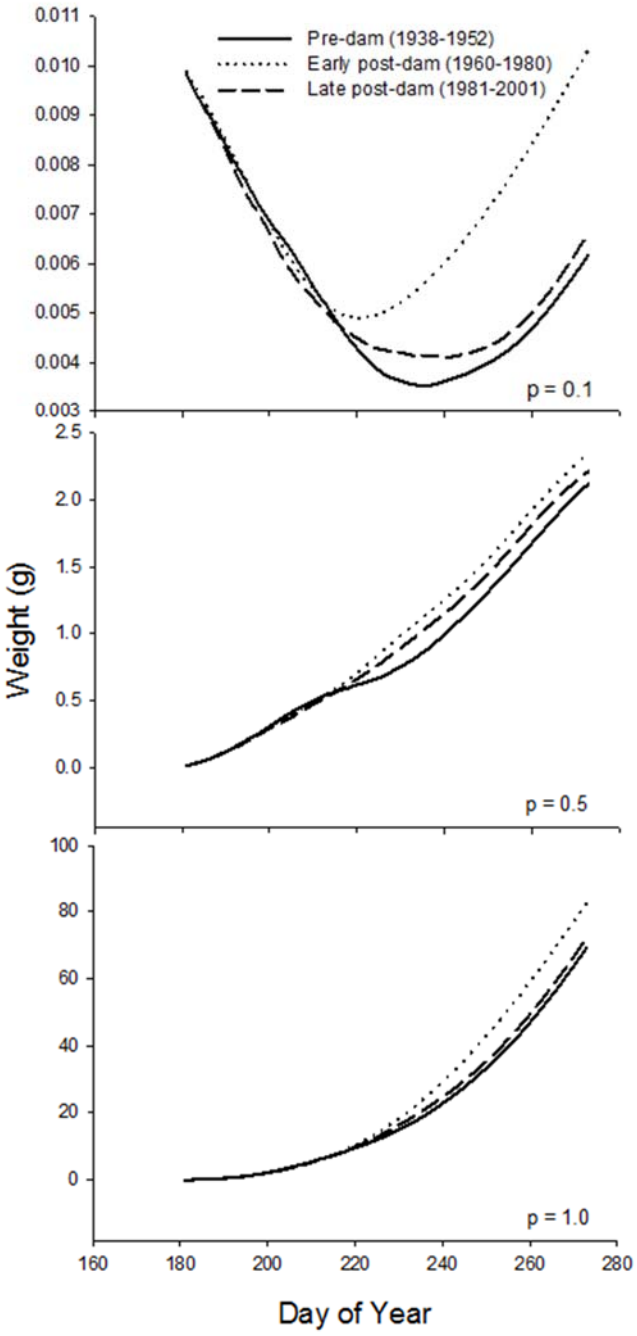
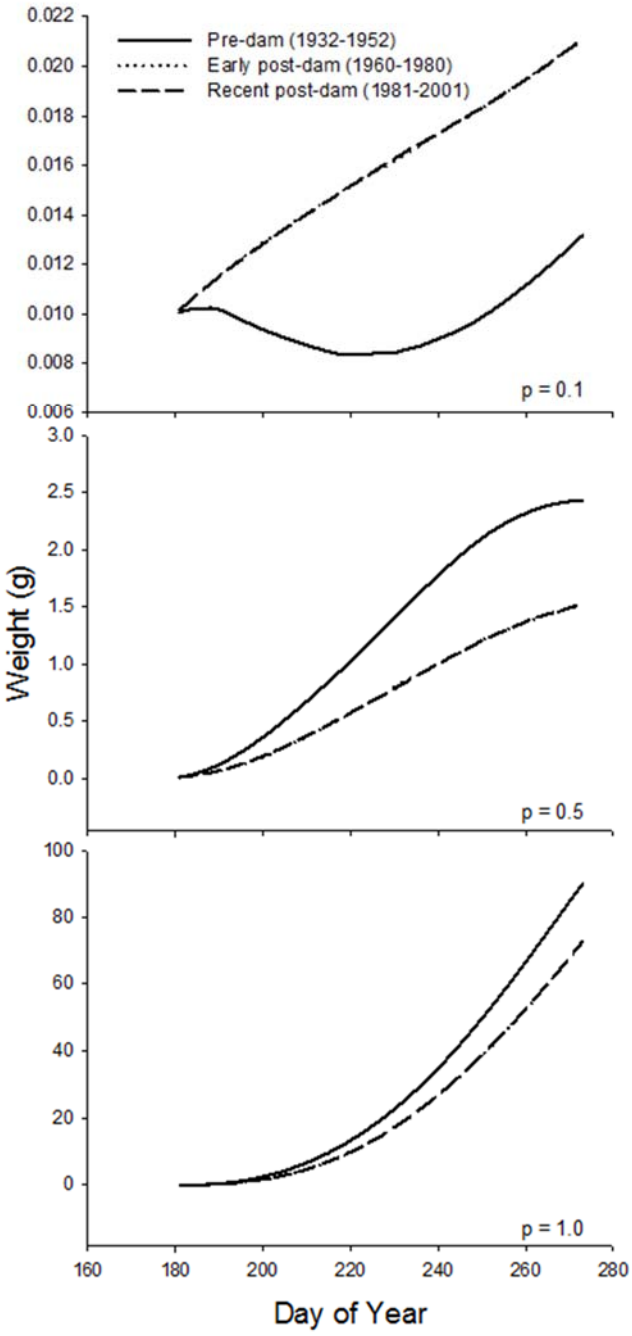


Figure 6. Stocked simulation scenario showing the weight accumulation throughout the three time periods in the Garrison Reach (GR). Graphs are in increasing order of feeding rates with p-values correlating to the proportion of maximum consumption where p = 1 is equivalent to feeding at 100% consumption rate.



CHAPTER 4. SUMMARY AND RESEARCH NEEDS

Summary

Larval Pallid Sturgeon (*Scaphirhynchus albus*) and the factors affecting their survival are poorly understood (Kallemeyn 1983). The outcome of this research has improved our understanding of the larval Pallid Sturgeon's physiological requirements within the Missouri River basin. Modeling output revealed reasonable estimates of growth rates and feeding rates when compared with independent laboratory observations. Using the bioenergetics model, biologists may now estimate growth rate of larval Pallid Sturgeon as it relates to prey compostion, feeding rate, and water temperature. The versatility in model usage makes it a practical tool for biologists and managers to use when assessing habitat requirements and priortizing recovery actions.

Using the bioenergetics model, I simulated the effects of downstream thermal suppression through hypolimnetic dam release. Results indicate major differences in growth potential due to decreased temperatures in the first 110 km below Garrison Dam; however, these effects are neglibible at 1880 km. In Garrison Reach (GR), growth was suppresed by 187% and 60% in Natural Spawning Simulation and Stocking Simulation, respectively. Temperature suppression accounts for a 115% and 31% difference in cumulative thermal units in the Natural Spawning Simulation and Stocking Simulation. Alternative methods of dam regulation, such as selective withdrawal using surface-layer water, may help to mitigate the effects thermal suppression.

Research Needs

1) Shovelnose Sturgeon (*Scaphirhynchus platorynchus*) larvae or unidentified *Scaphirhynchus* spp. are occasionally used as a surrogate for larval Pallid

Sturgeon in assessing habitat use and constructing management decisions due to their relatively high abundance (USFWS 2003; Phelps et al. 2010; Phelps et al. 2012). Although closely related, Pallid Sturgeon and Shovelnose Sturgeon are genetically different from each other and throughout their range (Schrey et al. 2011). Both species also differ in respect to drift velocity and time to settling (Braaten et al. 2008). Conversely, temperature effects on embryonic development are extremely similar (Kappenman et al. 2013). Future research should parameterize the larval Shovelnose Sturgeon bioenergetics model to evaluate when these two *Scaphirhynchus* spp. can be used interchangeably.

2) Hypolimnetic dam releases have been shown to constrain the success of downstream native fishes (Clarkson and Childs 2000). To simulate these effects, I estimated the differences in larval Pallid Sturgeon growth based solely on historical versus contemporary temperature averages. In the Garrison Reach (GR), thermal suppression was evident and resulted in dramatic differences in end weight. Thermal effects of hypolimnetic releases have been found to suppress temperatures below these dams as far as 300 km downstream (Everett et al. 2003). Future research should assess the seasonal geographic extent of thermal suppression by estimating its effects on larval Pallid Sturgeon growth potential.
3) The Army Corps of Engineers were mandated to restore shallow water habitat to aid in recovery of the Pallid Sturgeon population (USFWS 2003). Despite increased research, data regarding habitat use and requirements for larval and young-of-year Pallid Sturgeon have been lacking (USFWS 2014).

Macroinvertebrate densities have been measured in some sections of the Missouri River (Grohs 2008; Hay et al. 2008); however, prey availability within recovered shallow-water habitat is currently unknown. Future research should use the bioenergetic model developed in this study to evaluate probability of larval Pallid Sturgeon growth and survival in recovered shallow-water habitat.

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